

CYTOGEOGRAPHY OF PHACELIA RANUNCULACEA (HYDROPHYLLACEAE)

TSAN IANG CHUANG AND LINCOLN CONSTANCE

Both the occurrence of a disjunct pattern of distribution and the existence of markedly different cytotypes (or chromosome numbers) in the same species are items of considerable interest. When the two phenomena are combined, as they are in *Phacelia ranunculacea* (Nuttall) Constance, the data are worthy of record.

Phacelia ranunculacea (Plate 1) first entered the literature as *Ellisia ranunculacea*, described in 1837 by Nuttall from material that he obtained "in the shady humid alluvial forests of the Arkansas" (Constance 1940, 1949). Since this material was collected and apparently mixed with plants of *Ellisia microcalyx* Nuttall secured at the same time and place, it is not surprising that Gray confused and combined the two under what was known as *Nemophila microcalyx* (Nuttall) Fisch. & Mey. (= *N. triloba* (Raf.) Thieret (1970) = *N. aphylla* (L.) Brummitt (1972) — a singularly inappropriate epithet!). When Watson described *Phacelia covillei* from the Potomac River near Washington, D. C., in 1890, he had no occasion to identify this with a midwestern plant or to seek an earlier epithet in the synonymy of *Nemophila*. The consanguinity of the two entities was postulated by the junior author in 1940, and he included *Phacelia ranunculacea* in his subsequent revision of *Phacelia* subg. *Cosmanthus* (1949).

Chromosome numbers for *Phacelia* subg. *Cosmanthus* were ascertained and published some twenty-five years ago (Cave & Constance 1947, 1950; Constance 1949, 1950, 1963) and many of them were confirmed later by Gillett (1964, 1968), by Murdy (1966), and by the senior author (unpublished). Of the eleven species reported, seven had $n = 9$, one had $n = 8$, two had $n = 5$, and *P. ranunculacea* had $n = 14$. Constance remarked with regard to the last: "The arithmetical possibilities of synthesizing *P. ranunculacea*, with 14 pairs, from *P. maculata* or *P. dubia* (both with 5 pairs) and some 9-paired species are very attractive, but it is difficult to see whence one could derive the morphological characteristics that make *P. ranunculacea* so distinctive a plant" (1949, p. 10). Wilson characterized the species as "peculiar in its tubular-campanulate corolla, vestigial glands, semiglobose seeds, chromo-

some number, and disrupted distribution . . ." (1960, p. 203). Gillett (1968) placed *P. ranunculacea* in a class (Group I) by itself because of its unequally inserted stamens and unique chromosome number. He also suggested that it is closer to the genus *Nama* than to *Phacelia* and predicted that it "ultimately will be recognized as a monotypic genus" (1968, p. 371).

The latter prediction may indeed prove to be true, but the designation of yet another monotypic genus of Hydrophyllaceae — there already are five — does not promise to shed much additional light on relationships. The resemblances to *Ellisia* and *Nemophila* are superficial and depend upon similarity in habit and habitat and in size and shape of corolla. Although the relation of corolla and androecium might suggest *Nama*, the foliage, style and seeds are not compatible with this reference. The genus *Phacelia*, as currently treated, is certainly polymorphic and the placing of emphasis on internal differences could readily lead to generic fragmentation. Conversely, stressing similarities makes it possible to retain this taxon as a large morphologically and cytologically diverse but apparently "natural" grouping, at least until further evidence, perhaps from palynology or biochemistry, leads to a more satisfactory division.

While making a floristic foray into southern Illinois in the spring of 1968, the senior author and his wife obtained vegetative material and buds of plants which appeared referable to *Phacelia*. When the buds revealed an unexpected chromosome count of $n = 6$, vegetative material was sent to both Gillett and Constance. The latter associated it very tentatively with *P. ranunculacea*, but emphasized the need of flowers and fruit for any positive identification, especially in view of the cytological findings. Complete specimens obtained in Illinois and neighboring states in subsequent years (1969–1973) confirmed the tentative identification. All of these collections proved to have 6 pairs of chromosomes.

These findings raised the possibilities that either there was error in the chromosome number originally reported (which was, after all, based upon a single collection) or that there were undetected morphological differences between the Maryland and the midwestern populations. Successful efforts to obtain East Coast material made it possible to grow the two geographically separated populations together in the greenhouse at Normal,

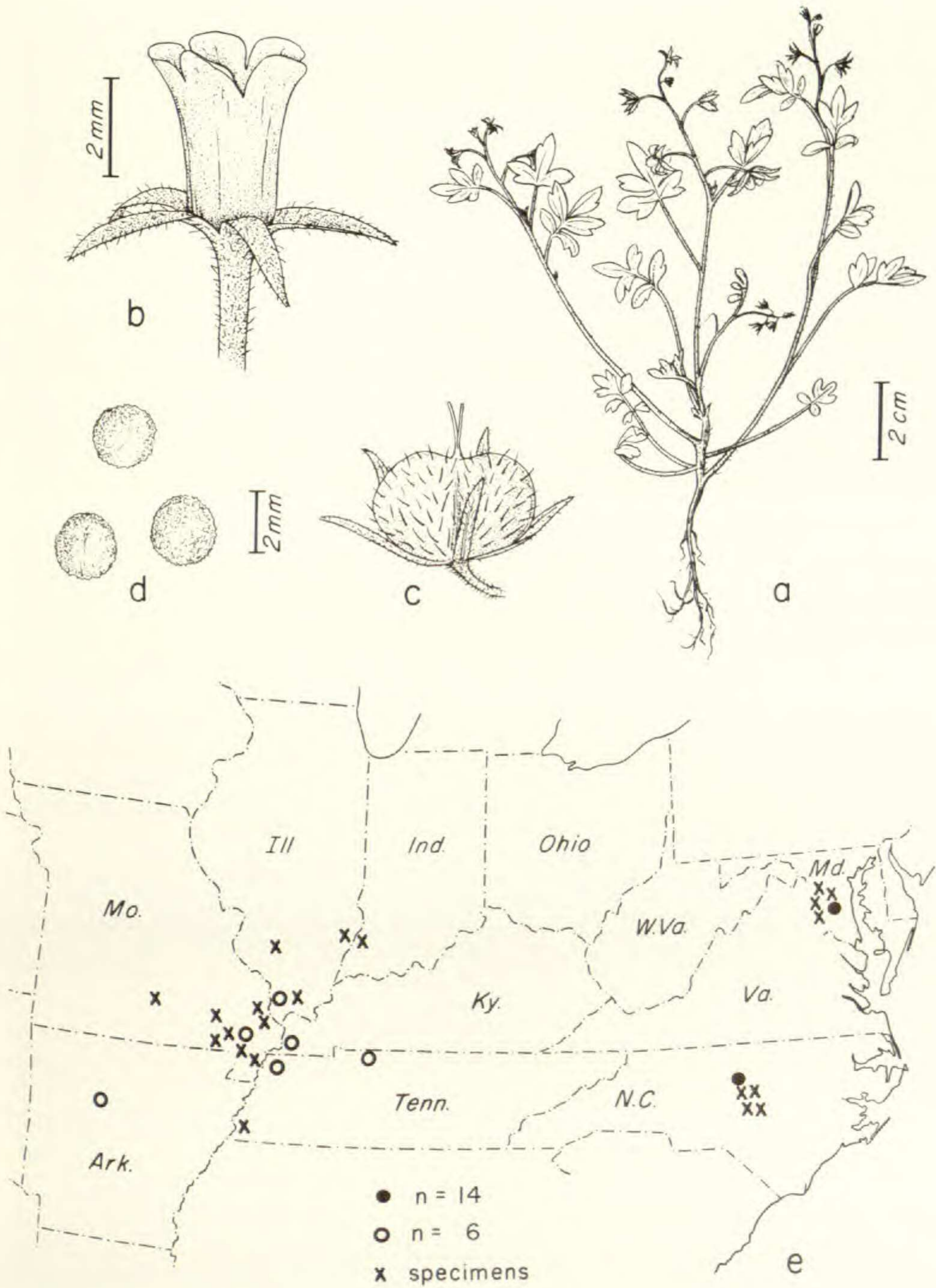


Plate 1. *Phacelia ranunculacea*. a, habit; b, corolla; c, capsule; d, seeds; e, distribution map. (From Chuang & Chuang 7240, 6851, and 6856.)

Illinois, and to confirm the reported chromosome count of $n = 14$ on Maryland and North Carolina plants. The new cytological information may be summarized as follows:

$n = 6$

Illinois. UNION CO.: Pine Hill, *Chuang & Chuang* 6180, 6608, 6755, 6858, 7240

Missouri. STODDARD CO.: Agilla, *Chuang & Chuang* 6758

Tennessee. MONTGOMERY CO.: Clarksville, *Chuang & Chuang* 6854

OBION CO.: Walnut Log, *Chuang & Chuang* 6855

Kentucky. HICKMAN CO.: Columbus, *Chuang & Chuang* 6856

Arkansas. POPE CO.: Russellville, *G. Tucker* 8478

$n = 14$

Maryland. MONTGOMERY CO.: Plummers Island, *J. J. Wurdack* 2632, *Chuang & Chuang* 6850

North Carolina. CHATHAM CO.: Haw River, *Chuang & Chuang* 6851

At first it was believed that it might be possible to find at least micro-morphological criteria for separating eastern from mid-western populations, but this prospect diminished with continued investigation in field and in greenhouse. No consistent morphological distinction has been found between the two cytotypes, the pollen and karyotypes of which are shown in Plate 2. The very small size of the tubular-campanulate corollas (exceptional in *Phacelia* and unique in subgenus *Cosmanthus*) and the inclusion of the stamens have unfortunately frustrated all attempts to hybridize members of the two cytotypes.

The known distribution of *Phacelia ranunculacea* is shown in the accompanying map (Plate 1e). No exact replica of this pattern has been found. Fernald (1950) suggested that *P. ranunculacea* is "Probably of more general range; easily overlooked or mistaken for *Ellisia nyctelea*" (p. 1194), but this appears to be an inadequate explanation. In his interesting article on Virginia species with disjunct populations in the Midwest, Harvill (1969) lists *P. ranunculacea* as one of only three species primarily of the Atlantic Coastal Plain and restricted in the Midwest to lowland areas. (The other two species are the grass, *Distichlis spicata* (L.) Greene, and the orchid, *Isotria medeoloides* (Pursh) Raf.). He attributes such distributional patterns to migrations in various directions and subsequent contractions of range under changing

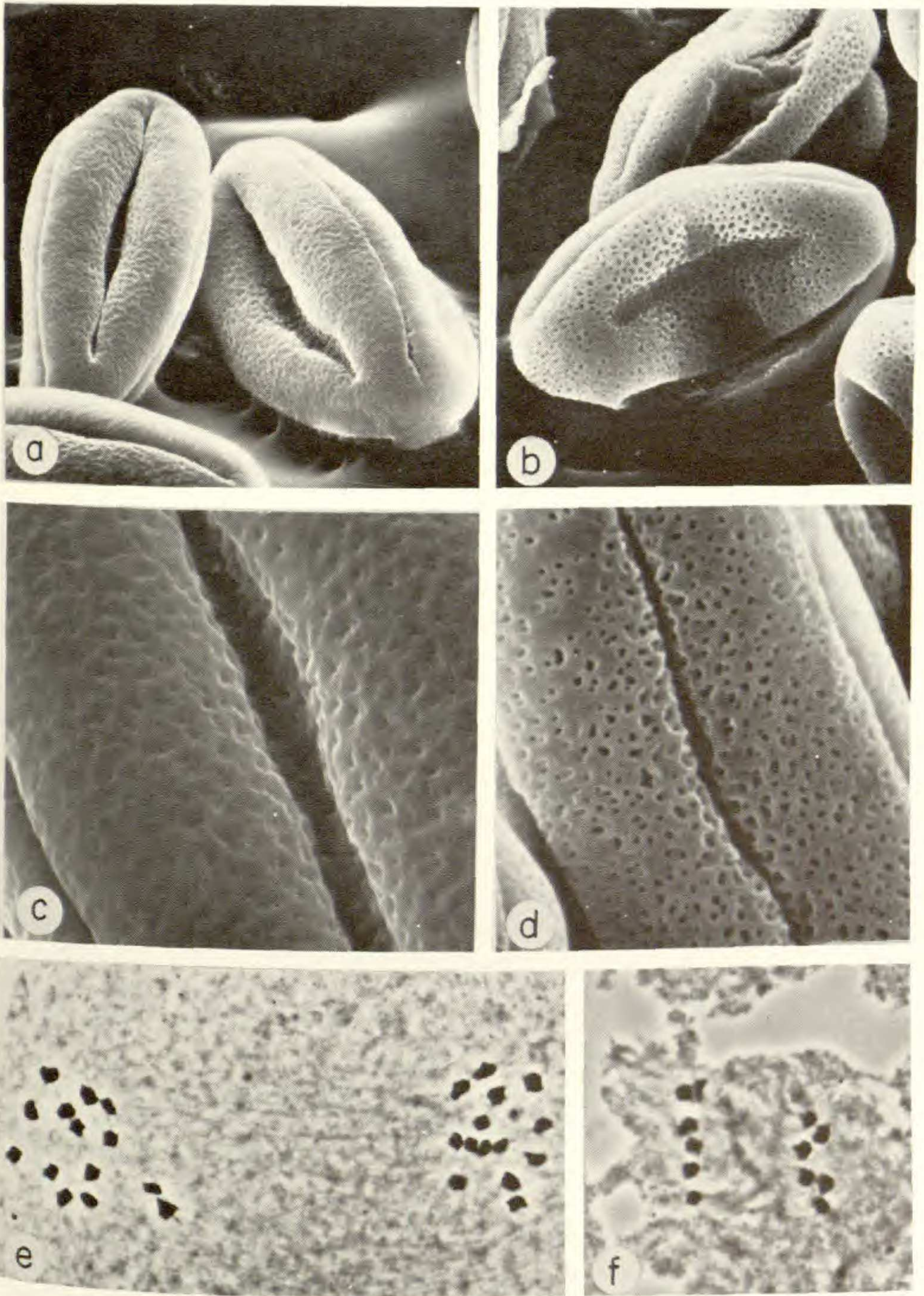


Plate 2. *Phacelia ranunculacea*. Pollen and karyotypes. a, pollen of 6851, $\times 1500$; b, pollen of 6854, $\times 1500$; c, pollen surface of 6851, $\times 3600$; d, pollen surface of 6855, $\times 3600$; e, karyotype of 6851, $\times 880$; f, karyotype of 6755, $\times 880$. (All Chuang & Chuang collections, collection data given in the preceding tabulation.)

climatic and physiographic conditions. Such interrupted ranges, he believes, "go far back in geologic time" (p. 229).

Wiggins (1936) indicated that *Iliamna remota* Greene was known from only two stations: an island in the Kankakee River in Illinois, and the summit of Peter's Mountain in Virginia. There is now an additional Virginia station from the James River (Wood, personal communication). The distribution of *Lysimachia radicans* Hook. as mapped by Ray (1956), occurring "in the lower Mississippi River Valley and [with] apparent isolation in Virginia," shows a slight similarity.

Terrell indicates that *Houstonia tenuifolia* Nuttall (= *Hedyotis nuttalliana* Fosberg) possesses an Ozark-Ouachita center and an Appalachian center. "In general, the degree of [morphological] overlap is so great that I have preferred not to distinguish plants of the two centers as separate subspecies, but consider them all part of one variable species. . . . It appears that populations in these two centers have been isolated from each other for a rather long time, long enough for certain differences to arise" (1959, p. 192). Lewis and Terrell (1962) found that populations throughout the range of the species had a chromosome complement of $n = 6$, i.e. diploid.

Carroll Wood has generously called to our attention several other cases of striking disjunction. *Alnus maritima* (Marshall) Nuttall, which may or may not be conspecific with east Asian alders, occurs near the coast of Delaware and Maryland, and then again in southern Oklahoma. Woodson, in his monographic study of the genus *Asclepias* (1954), lists no fewer than eight "bicentric species" of milkweeds, whose occurrence he relates to his Appalachian and Ozarkian centers. The rare *Cotinus obovatus* Raf. is known from Alabama, Tennessee, Arkansas, Oklahoma, and the Edwards Plateau of Texas (Brizicky, 1962). The likewise scarce *Neviusia alabamensis* A. Gray is known from Alabama, Arkansas, and Missouri (Robertson, 1974). None of these, however, offers a strict parallel to the distribution of *Phacelia ranunculacea*.

In *Parthenium hispidum* Raf., Rollins (1950) discovered that var. *hispidum* of the Mississippi Valley appears to be a tetraploid ($2n = 72$), whereas var. *auriculatum* (Britt.) Rollins of the Virginia and North Carolina piedmont appears, on circumstantial evidence, to be diploid ($2n = 36$). If the complements of $n = 6$ and

$n = 14$ can be thought to have any polyploid relationship, then this is the reverse of the *Phacelia ranunculacea* situation, where the inland populations have the smaller chromosome number.

But as Wood (1971, p. 371) thoughtfully reminds us, "a paper like this is not supposed to have definite conclusions, for the basic purpose is to present taxonomic and distributional data . . .", and hopefully some food for thought.

ACKNOWLEDGMENTS

We would like to express our appreciation to all those persons who assisted in the furtherance of this project, but would like particularly to mention the following: R. B. Burton, Jonesboro Ranger Station, U. S. Forest Service, Jonesboro, Ill.; E. W. Chester, Austin Peay State University, Clarksville, Tenn.; John A. Churchill, National Institutes of Health, Bethesda, Md.; Gary Tucker, Arkansas Polytechnic College, Russellville, Ark.; Carroll E. Wood, Jr., Arnold Arboretum and Department of Biology, Harvard University, Cambridge, Mass.; John J. Wurdack, National Museum of Natural History, Smithsonian Institution, Washington, D. C.

LITERATURE CITED

- BRIZICKY, G. K. 1962. The genera of Anacardiaceae in the southeastern United States. *Jour. Arnold Arb.* **43**: 359-375.
- CAVE, M. S., & L. CONSTANCE. 1947. Chromosome numbers in the Hydrophyllaceae: III. *Univ. Calif. Publ. Bot.* **18**: 449-465.
- & ———. 1950. Chromosome numbers in the Hydrophyllaceae: IV. *Univ. Calif. Publ. Bot.* **23**: 363-382.
- CONSTANCE, L. 1940. The genus *Ellisia*. *Rhodora* **42**: 33-39.
- . 1949. A revision of *Phacelia* subgenus *Cosmanthus* (Hydrophyllaceae). *Contr. Gray Herb.* **68**: 1-48.
- . 1950. Some interspecific relationships in *Phacelia* subgenus *Cosmanthus*. *Proc. Am. Acad.* **78**: 135-147.
- . 1963. Chromosome number and classification in Hydrophyllaceae. *Brittonia* **15**: 273-285.
- FERNALD, M. L. 1950. *Gray's manual of botany*. Ed. 8. American Book Co., New York. 1632 pp.
- GILLETT, G. W. 1964. Genetic barriers in the *Cosmanthus phacelias* (Hydrophyllaceae). *Rhodora* **66**: 359-368.
- . 1968. Systematic relationships in the *Cosmanthus phacelias* (Hydrophyllaceae). *Brittonia* **20**: 368-374.

- HARVILL, A. M., JR. 1969. Virginia species with disjunct populations in the Middle West. *Castanea* **34**: 225-229.
- LEWIS, W. H., & E. E. TERRELL. 1962. Chromosomal races in eastern North American species of *Hedyotis* (*Houstonia*). *Rhodora* **64**: 313-323.
- MURDY, W. H. 1966. The systematics of *Phacelia maculata* and *P. dubia* var. *georgiana*, both endemic to granite outcrop communities. *Am. Jour. Bot.* **53**: 1028-1036.
- RAY, J. D., JR. 1956. The genus *Lysimachia* in the New World. Ill. Biol. Mon. **24**: 1-160.
- ROBERTSON, K. R. 1974. The genera of Rosaceae in the southeastern United States. *Jour. Arnold Arb.* **55**: 344-401.
- ROLLINS, R. C. 1950. The guayule rubber plant and its relatives. *Contr. Gray Herb.* **172**: 1-173.
- TERRELL, E. E. 1959. A revision of the *Houstonia purpurea* group (Rubiaceae). *Rhodora* **61**: 157-180, 188-207.
- WIGGINS, I. L. 1936. A resurrection and revision of the genus *Iliamna* Greene. *Contr. Dudley Herb.* **1**: 213-229.
- WILSON, K. A. 1960. The genera of Hydrophyllaceae and Polemoniaceae in the southeastern United States. *Jour. Arnold Arb.* **41**: 197-212.
- WOOD, C. E., JR. 1971. Some floristic relationships between the southern Appalachians and western North America. In P. C. HOLT, ED. The distributional history of the biota of the southern Appalachians. Res. Div. Mon. 2, Virginia Polytechnic Institute and State University, Part II, pp. 331-404.
- WOODSON, R. E. 1954. The North American species of *Asclepias* L. *Ann. Mo. Bot. Gard.* **41**: 1-211.

T. I. C.

DEPARTMENT OF BIOLOGICAL SCIENCES
ILLINOIS STATE UNIVERSITY
BLOOMINGTON-NORMAL, ILLINOIS 61761

L. C.

DEPARTMENT OF BOTANY
UNIVERSITY OF CALIFORNIA
BERKELEY, CALIFORNIA 94720